FOOD AND ECOLOGICAL SYSTEMS MODELLING JOURNAL

Food and Ecological Systems Modelling Journal 6: e149273 (2025)
DOI: https://doi.org/10.3897/fmj.6.149273

Research Article

Landscapes from the bee perspective: an application of SolBeePop to field study data

Amelie Schmolke[1,2], Nika Galic[3], Silvia Hinarejos[4]

1 *RIFCON GmbH, Hirschberg, Germany*
2 *Waterborne Environmental, Leesburg, Virginia, USA*
3 *Syngenta Crop Protection AG, Basel, Switzerland*
4 *Sumitomo Chemical, Saint Didier au Mont d'Or, France*

Corresponding author: Amelie Schmolke (amelie.schmolke@rifcon.de)

Abstract

Introduction: The temporal and spatial pattern of floral resources in a landscape is an important driver of dynamics of pollinator species, such as solitary bees. Thus, the representation of complex landscapes in models is of interest when assessing whether landscapes could provide sufficient resources to sustain populations of solitary bee species. The consideration of landscape compositions is also important when estimating exposures to pesticides and their potential effects on managed and natural populations. At the same time, information on the use of complex landscapes by solitary bees is lacking for most species. This challenges the inclusion of this important aspect into models representing bee species and model applications for risk assessment and management.

Methods: In the current paper, we tested options to include different levels of information available to represent compositions of agricultural landscapes. We applied the population model for solitary bees, SolBeePop, to simulate untreated control trials from field studies conducted with *Osmia bicornis*, compared model outputs to study data and assessed model performance using different scenarios. First, we reviewed literature reporting pollen compositions of bee-collected brood provisions for *O. bicornis*. As studies were conducted in a range of different landscapes and geographical regions, generalised floral preferences of the species could be derived.

Results: In aggregating land-cover information using increasingly detailed information, we showed that the consideration of multiple resources across the landscape and study period improved the model performance in representing the field study data. At the same time, we demonstrated that simplified, conservative scenarios can be generated and evaluated with the model if information is lacking on species' preferences as well as resource distributions in time and space.

Conclusions and relevance: The representation of complex landscapes using different levels of detail makes SolBeePop a flexible tool for simulating solitary bee populations in agricultural landscapes using often limited information, thereby supporting ecological risk assessment and management.

Key words: floral resources, landscape composition, *Osmia bicornis*, population model, solitary bees

OPEN ACCESS

Academic editor: Christopher John Topping
Received: 10 February 2025
Accepted: 13 May 2025
Published: 17 June 2025

Citation: Schmolke A, Galic N, Hinarejos S (2025) Landscapes from the bee perspective: an application of SolBeePop to field study data. Food and Ecological Systems Modelling Journal 6: e149273. https://doi.org/10.3897/fmj.6.149273

Copyright: © Amelie Schmolke et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

The composition and configuration of landscapes plays a crucial role in the abundance and diversity of species (Hopfenmüller et al. 2014; De Palma et al. 2015; Bottero et al. 2023). This is especially true in agroecosystems which are, by their nature, very dynamic and are composed of agricultural fields and semi-natural areas, mixed at different scales and proportions. For pollinators, such as wild bees, the spatial configuration of a landscape is as important as the temporal aspect due to their specific phenology and dependence of their reproductive output on floral resources (Mandelik et al. 2012; Scheper et al. 2015; Persson et al. 2018; St. Clair et al. 2020; Ammann et al. 2024). Wild bees, specifically solitary bees, have unique life cycles with relatively brief periods of activity whereby single females are active between two and eight weeks and use the landscape to collect pollen and nectar to provision their brood. Most solitary bees construct nests composed of separate cells – in soil or above-ground cavities – in which a single egg is laid after a provision is collected. The number of brood cells per female is driven by multiple factors, including, for example, the species, the availability of floral resources during the active period, the weather and the availability of suitable nest sites. The suitability of a landscape as habitat for a wild bee species therefore depends on the species' phenology, floral preferences, foraging radius and nesting strategy. However, we still have a relatively limited understanding how these factors interact and drive abundances of solitary bee populations. For instance, mass-flowering crops can be beneficial for bees, but resource limitation before or after crop flowering can be detrimental (Yourstone et al. 2021; Bishop et al. 2024; Riggi et al. 2024).

For ecological risk assessment of agrochemicals, a better understanding of how bees use dynamic landscapes in agroecosystems is important to evaluate any potential for exposures to pesticides (EFSA et al. 2023). However, landscape composition alone may not be a good predictor of exposure (Bednarska et al. 2022; Knapp et al. 2023; Nicholson et al. 2024), as other factors, such as food and nesting availability or weather, can influence exposure and, ultimately, risk to pollinators. Furthermore, promoting landscapes that enhance and preserve biodiversity of pollinators and other species is of much interest to conservationists, risk managers and the public. Due to the myriad of important factors, as well as their various interactions, in silico tools, such as ecological models, are better suited than empirical approaches to evaluate the role of various factors as well as management strategies. Models of bee populations represent comprehensive and integrative approaches whereby various landscape representations can be implemented and interactions between species' populations and landscape factors can be tested systematically (Becher et al. 2014, 2018).

Landscapes and resource availabilities in ecological models can be captured at different levels of detail. Thereby, the level of detail requires correspondingly detailed understanding of the system and data to provide information for model parameterisation and testing. Fully spatially explicit models usually represent the landscape in two dimensions at varying resolutions. Resources can be linked to specific locations in the simulated landscape and may either be determined via an input, a simplified rule or resource regrowth

may be explicitly simulated in a submodel (Grimm and Railsback 2005; Accolla et al. 2021). Detailed information about each resource in the landscape and its temporal dynamics are required as well as the spatial behaviour of the species using the resource, but such detailed data are lacking for most species of interest. Even for the honey bee, a species with a large body of research on its foraging and floral preferences, translating landscape composition data to resource availability in time and space still remains difficult (Schmolke et al. 2019; Lau et al. 2023). Across solitary bee species, data on floral resource use and foraging behaviour are much more limited than for the honey bee if available at all. One exception is the red mason bee, *Osmia bicornis*, which represents an excellent case example because multiple studies have been published that identify pollen collected by the bees for brood provision in various regions across its range (see Floral preferences of *O. bicornis* and Table 1). Red mason bees are polylectic bees, foraging on flowers from a range of plant taxa in contrast to some solitary bee species that are specialised on a single or few plant taxa (oligolecty) (Danforth et al. 2019).

The main objective of our study was to demonstrate how a complex agricultural landscape can be represented and aggregated to reflect the resource availability from the perspective of solitary bee species. To this end, we applied an existing population model for solitary bees, SolBeePop (Schmolke et al. 2023, 2024), to simulate field studies conducted with the red mason bee. SolBeePop is a trait-based population model that can be applied to simulate a range of solitary bee species, using their ecological traits as model parameters. The individual-based model simulates individual bees and uses a daily time step. Input time series capture the impacts of daily weather and resource availabilities from crop and non-crop floral resources in the landscape. Thus, SolBeePop is not a spatially explicit model, but uses an input that aggregates resource availability in the landscape to daily time series with the aim to simplify scenarios representing realistic landscapes, which can be especially useful when data on resource distribution in the landscape and spatial behaviour are lacking. Resources are grouped into two types: crops (or treated floral resources in case pesticide exposures are considered) and mixed, (semi-)natural floral resources (where no pesticide exposure is assumed). In the current study, we focused on the aggregated representation of the landscape and how it impacts model outputs. Thus, we did not simulate pesticide exposures, but focused on untreated control fields from available field studies conducted with *O. bicornis* (Ruddle et al. 2018). We developed input time series for the landscapes surrounding six control field study locations whereby we used different levels of information available for the locations and assessed whether and how more detailed data on floral resource availability in the landscape could improve the representation of study data by the model. The pollen composition of provisions was analysed in the field studies used in the simulations (Ruddle et al. 2018). Thus, different levels of complexity of data specific to the species, study locations and timing were used and compared in simulations with SolBeePop. In addition, we address the importance of data which provided information on the weather-dependent foraging preferences of the simulated bees. We discuss the implications of the simulation study for the representation of other solitary bee species and the simulation of exposures and effects of pesticides.

Floral preferences of *O. bicornis*

We reviewed the literature for information on floral preferences of polylectic solitary bees with the focus on *O. bicornis*. Polylectic bee species collect pollen and nectar from a range of plant species for the provisioning of their brood. Although not specialised on a specific plant taxon, polylectic bees do exhibit preferences for some floral resources rather than collecting pollen and nectar indiscriminately from plants blooming in their surroundings (Bosch et al. 2001; Danforth et al. 2019). However, the preferences of polylectic solitary bee species are often not well known because they require analysis of pollen composition of brood provisions across habitats. Most published studies reporting pollen compositions of brood provisions focus on Megachilidae bees, including species of the genera *Megachile* and *Osmia* (Raw 1974; Cripps and Rust 1989; O'Neill et al. 2004; Teper 2008; O'Neill and O'Neill 2011; Gresty et al. 2018; Nagamitsu et al. 2018; Söderman et al. 2018; Bertrand et al. 2019; Killewald et al. 2019; Vaudo et al. 2020). The most data on pollen compositions were found for the red mason bee, *O. bicornis* L., a polylectic, solitary bee species native to Europe and an important pollinator of crops (Bosch et al. 2008). The bee is active in the spring when the females collect pollen and nectar to provision brood cells in existing above-ground cavities. Studies reporting pollen compositions of *O. bicornis* provisions were conducted in multiple regions in Europe, including locations in Poland, Czechia, Germany, Sweden, Switzerland and Great Britain (Raw 1974; Teper and Bilinski 2009; Jauker et al. 2012; Haider et al. 2014; Peters et al. 2016; Gresty et al. 2018; Persson et al. 2018; Ruddle et al. 2018; Söderman et al. 2018; Bertrand et al. 2019; Ryder 2019; Šlachta et al. 2020; Splitt et al. 2021; Yourstone et al. 2021; Bednarska et al. 2022; Misiewicz et al. 2023). Landscapes were mostly agricultural with several studies conducted in areas with oilseed rape fields. However, landscape compositions and the availability of various flowering crops and wild plant species varied widely between studies. Thus, the plant taxa identified from the bee-collected pollen provided a general picture of the floral preferences of *O. bicornis* independent of floral resources available at a single location.

We compiled the reported pollen compositions from the studies of *O. bicornis* and summarised the findings (Table 1). Thereby, we summarised reported plant species into higher-level taxa because pollen was identified to various taxonomic levels within and across studies. Pollen from oak (*Quercus*), Brassicaceae (including oilseed rape) and buttercups (Ranunculaceae) were commonly found in *O. bicornis* provision samples in all studies. In addition, pollen from Rosaceae (including non-cultivated as well as orchard trees and berries) and other tree species were reported across most studies. We further compared the studies reporting pollen compositions of *O. bicornis* provision samples quantitatively across identified plant taxa (Peters et al. 2016; Persson et al. 2018; Ruddle et al. 2018; Bertrand et al. 2019; Ryder 2019; Splitt et al. 2021; Yourstone et al. 2021; Bednarska et al. 2022; Misiewicz et al. 2023). The three most commonly observed plant taxa (*Quercus*, Brassicaceae and Ranunculaceae) also were the ones making up a high percentage (> 50%) of pollen in some samples. In studies that sampled brood provisions at multiple time points, pollen compositions shifted during the study period, reflecting the flowering phenology of the plant species (Persson et al. 2018; Ruddle et al. 2018; Bertrand et al. 2019; Ryder 2019; Yourstone et al. 2021; Bednarska et al. 2022). Percentages of

Brassicaceae pollen (identified in the studies as Brassicaceae, *Brassica* or *Brassica napus* = oilseed rape) in *O. bicornis* provision samples ranged from 0% to 73% across studies providing detailed sample composition data. In four studies, flowering oilseed rape fields in the landscape were explicitly part of the study design (Peters et al. 2016; Ruddle et al. 2018; Yourstone et al. 2021; Bednarska et al. 2022). *O. bicornis* were released at nest boxes within or adjacent to flowering oilseed rape fields or at defined distances from the fields. In these studies, the average and maximum proportion of Brassicaceae pollen in provision samples was higher compared to the studies that did not focus on oilseed rape. For a quantitative comparison between studies, we assigned the reported pollen taxa to four categories: deciduous trees (not including Rosaceae), Brassicaceae (assumed to correspond mainly to oilseed rape, *Brassica napus*), Rosaceae (including, but not limited to, fruit/orchard trees and berries that may be cultivated) and non-cultivated herbaceous plants (including Ranunculaceae) (see Suppl. material 1). The proportion of pollen in provision samples originating from the four categories varied considerably and was likely strongly dependent on the study design, landscape composition and timing of the sampling. In most studies, deciduous trees (often mostly *Quercus*) made up the highest proportion on average (Persson et al. 2018; Ruddle et al. 2018; Bertrand et al. 2019; Splitt et al. 2021; Yourstone et al. 2021; Bednarska et al. 2022). However, Misiewicz et al. (2023) reported Brassicaceae at highest percentage across samples, Peters et al. (2016) Rosaceae pollen and Ryder (2019) non-cultivated herbaceous plants. Yourstone et al. (2021) did not identify any Rosaceae pollen in their samples and Brassicaceae pollen was absent or observed at very low proportion (< 3%) at some study sites from Ryder (2019), as well as Splitt et al. (2021). It should be noted that pollen from annual (field) crops other than Brassicaceae were uncommon in the review of *O. bicornis* pollen analyses. However, Ryder (2019) reported pollen from *Raphanus* (genus including cultivated radishes) in a subset of pollen samples, with a maximum of 70% of *Raphanus* pollen observed in a single sample. Bertrand et al. (2019) found pollen from the genus *Vitis* (including cultivated grapes) with sample proportions between 0 and 80%. Misiewicz et al. (2023) reported Poaceae pollen in some samples at proportions > 50%, but it was not resolved whether the pollen originated from cultivated cereals or other grasses. Poaceae were also reported making up 30% of pollen extracted from scopae of *O. bicornis* collection (museum) specimen (Haider et al. 2014). The information from the review of literature on pollen preferences of *O. bicornis* was used to generate the input to the SolBeePop model (see section Methods).

Methods

Description of *O. bicornis* field studies

For the simulations with SolBeePop, we used data from a set of six published field studies with *O. bicornis* (Ruddle et al. 2018) which were conducted in the context of pesticide risk assessments. Thereby, control nest boxes were installed in untreated oilseed rape fields and treatment nest boxes in fields treated with an insecticide, whereby field sizes ranged between 1.9 and 2.7 ha. For the purposes of the current study, we used only data from the untreated controls. In the studies, incubated *O. bicornis* cocoons were introduced at the nest boxes at the onset of

Table 1. Overview of plant taxa that were identified in samples from *O. bicornis* provisions across published studies. Taxa that occurred with ≥ 3% in at least one sample per study are indicated or listed as present if no quantitative data were provided. Pollen was identified to different taxonomic levels and we pooled data in larger groups as applicable. In Suppl. material 1, a detailed overview of the studies is provided and the studies providing quantitative data on pollen compositions are listed in detail.

References	*Quercus*	*Acer*	*Salix*	*Juglans*	*Aesculus*	Other trees [a]	Rosaceae [b]	Bassicaceae [c]	Ranunculaceae	*Lamium*	Asteraceae [d]	*Raphanus*	*Vitis*	Other herbaceous dicots [e]	Monocots [f]
Bednarska et al. (2022)	x	x	x	x		x		x	x					x	
Bertrand et al. (2019)	x	x	x	x	x	x	x	x	x		x		x	x	x
Gresty et al. (2018)							x		x	x				x	
Haider et al. (2014)	x	x					x	x	x					x	x
Jauker et al. (2012)	x				x		x	x	x						
Misiewicz et al. (2023)	x	x					x	x	x					x	x
Persson et al. (2018)	x	x	x		x		x	x	x						
Peters et al. (2016)	x	x					x	x	x	x					
Raw (1974)	x	x			x		x		x					x	
Ruddle et al. (2018)	x	x		x	x		x	x	x						
Ryder (2019) (Chapter 3)	x	x	x				x	x	x		x	x			
Söderman et al. (2018)											x				
Slachta et al. (2020)	x			x				x	x						
Splitt et al. (2021)	x	x	x	x	x	x	x	x	x					x	x
Teper and Bilinski (2009)	x	x	x	x	x	x	x	x	x	x	x				
Yourstone et al. (2021)	x	x						x	x						

[a] Woody species not included in any of the other categories, for example, *Carpinus*, *Fagus*, *Lonicera*, *Populus*, Rhamnaceae, *Ulmus*.
[b] Pollen origin reported as Rosaceae, Maleae, Pyreae, *Prunus*, *Rubus*, *Crataegus*.
[c] In studies focused on oilseed rape, pollen identified as *Brassica* or *B. napus*.
[d] Mostly *Centaurea* or *Taraxacum*.
[e] Herbaceous species not included in any of the other categories and include a large number of taxa.
[f] Mostly Poaceae or Cyperaceae.

oilseed rape flowering. After bee emergence, post-emergent female bees present in the nest boxes at night were monitored every three days along with the brood cells produced. At the end of oilseed rape flowering, the nest boxes were closed, preventing further nesting activity by the bees. Brood was brought into the laboratory over winter. A subset of cocoons was incubated to emergence in the following spring, with counts of female and male emergences reported.

Three studies were conducted in 2014 and the other three in 2015. Study sites in 2014 were near Kraichtal (Baden-Württemberg, Germany), Tübingen (Baden-Württemberg, Germany) and Fortschwihr (Alsace, France). In 2015, study sites were located near Niefern (Baden-Württemberg, Germany), Tübingen (Baden-Württemberg, Germany) and Celle (Niedersachsen, Germany). In 2014, 30 female and 60 male cocoons were introduced on a first introduction date and 120 female and 210 male cocoons were introduced three days later at each of the eight control nest boxes per study. In 2015, 60 female and 90 male cocoons were introduced on a single date at the eight control nest boxes per site. The percentage of females and males emerging from the introduced cocoons was recorded. In Suppl. material 2: table S1, the study locations and

dates are listed along with cocoons released and their emergence rates. In 2015, semi-field trials were conducted in addition to the field trials at the study sites (Ruddle et al. 2018). Those data were used previously for calibration and validation of SolBeePop (Schmolke et al. 2023). Although the semi-field trials were not the focus of the current paper, we show the study data in the plots for reference. Number of nesting females and cumulative brood cell production from the studies are plotted in Suppl. material 2: figs S1, S2).

SolBeePop model

We used the population model for solitary bees, SolBeePop (Schmolke et al. 2023, 2024), for the simulations of the field studies with *O. bicornis*. SolBeePop is a trait-based model capable of simulating different representative species of solitary bees, whereby species-specific trait values correspond to model parameters. The individual-based population model captures the life cycle of solitary bees. Each individual corresponds to a bee that passes through the life cycle from egg to active (post-emergent) adult in daily time steps. Developing bees (in-nest life stages) are assumed to consume their provision entirely and do not otherwise interact with their environment. Mortality occurs in the model at time of emergence of the adult bee, summarising the probability of death of pre-emergent life stages. Post-emergent females consume pollen and nectar on a daily basis. They reach maturity after a set time-span. At this time, they experience a chance of mortality that also represents bees dispersing from the simulated population and bees that never start nesting. Mature females produce offspring, based on a species-specific offspring production rate, resources available to provision the offspring and the nesting female's post-emergent age. Mature females have a daily chance of mortality and cannot live beyond a set maximum life span. Males are simulated by the model, but their interaction with the environment after emergence is not modelled explicitly. Post-emergent males die after a set life-span. Four daily time series (model inputs) determine the environmental conditions: weather-dependent foraging, floral resource availability from a focal crop or resource patch, resource availability from non-crop (e.g. mixed natural and semi-natural flowering plants) and the proportion of foraging on the focal crop. In combination, these time series define how much resource a female bee can collect from the landscape on a given day and, in turn, how efficiently she can provision brood cells. Accordingly, the model is not spatially explicit, but uses an aggregated landscape representation. An example input file can be found Suppl. material 2: table S9 and all input files used for the simulations in the current paper are available from Schmolke (2025). For the simulations presented in the current paper, we used the model version SolBeePop$_{ecotox}$ (Schmolke et al. 2024), but we did not simulate exposures or effects of pesticides. A detailed description of the model is available from Schmolke (2025).

Scenarios representing bee resources in the landscape

We generated three scenarios (model inputs) of resource availability in the landscape during the field phases of the six field studies, based on different assumptions and data (Table 2). From the field studies, detailed data were available that could provide information for the resource availability in the landscape (Ruddle

et al. 2018), including quantitative data on pollen composition of *O. bicornis* provisions from samples taken at 3–4 time points during the studies. Flowering growth stages (BBCH) of the focal oilseed rape field were reported (see Suppl. material 2: tables S2–S7). The landscape composition around the study locations was derived from satellite data. We generated SolBeePop input files, reflecting scenarios of floral resource availability in the landscape using increasingly detailed data. Table 2 provides an overview of assumptions and data used to generate the time series in the model input scenarios. For all scenarios, daily weather data were used, combined with the same assumptions about weather conditions amenable to foraging by *O. bicornis*. Weather-dependent foraging is addressed in more detail in section Weather-dependent foraging.

Table 2. Overview of data used to generate the time series in the SolBeePop input files dependent on scenario. Site- and study specific data were used for the field studies reported by Ruddle et al. (2018). General remarks are provided for the generation of each time series independent of study and bee species.

Time series in the input file	Description of time series	*Low detail* scenario	*Medium detail* scenario	*High detail* scenario	General remarks for scenario generation
Prop_foraging_day	The proportion of a given day available for foraging. This value reflects the daily weather and can take values between 0 (no foraging due to inclement weather) and 1 (bees can forage the maximum daily duration).	**Site-specific** weather data	**Site-specific** weather data	**Site-specific** weather data	Relevant (realistic) weather data should be used for simulations of study data or location-specific scenarios; daily (or higher frequency) weather data required
Quality_crop	Daily floral resource quality of a flowering, bee-attractive crop. The quality summarises the distance of the flowering crop from the nesting location and the resource availability within the patch (field). Values can range between 0 (no flowering crop within the foraging distance of the bee) and 1 (highly attractive flowering crop within short distance from nest the location).	**Study-specific** oilseed rape growth stages (BBCH)	**Study-specific** oilseed rape growth stages (BBCH)	**Study-specific** oilseed rape growth stages (BBCH)	Can be set to uniform value in the absence of study-specific data
Quality_nat	Daily floral resource quality of non-crop wildflower resources within the foraging range of the bee. The quality summarises the distance of the areas with flowers from the nesting location and the resource availability within the (closest and/or most attractive) areas. Values can range between 0 (no non-crop flowers within the foraging distance of the bee) and 1 (highly attractive flowers within short distance from the nest location).	Uniformly set to 0 as **simplifying, conservative assumption**	1) "prop:" **site-specific** area of land cover classes within three assumed foraging radii corresponding to *O. bicornis* preferences; 2) "dist:" **site-specific** shortest distance to each land-cover class corresponding to *O. bicornis* preferences	1) "prop:" **site-specific** area of land-cover classes within three assumed foraging radii corresponding to *O. bicornis* preferences; 2) "dist:" **site-specific** shortest distance to each land cover class corresponding to *O. bicornis* preferences	Site-specific data on plants flowering (relevant for the simulated bee species) in the surrounding of the nest sites can also be used if available
Prop_foraging_crop	Daily proportion of foraging on crop. The foraging on wildflower (non-crop) resources corresponds to (1 – Prop_foraging_crop).	Uniformly set to 1 as **simplifying, conservative assumption** (corresponds to foraging only on crop)	Uniformly set to 0.73 as **simplifying assumption**; this value corresponds to the highest proportion of *Brassica* pollen observed in *O. bicornis* provisions across studies	**Study- and site-specific** proportion of *Brassica* pollen in *O. bicornis* provisions	Study- and site-specific data on foraging activity of the simulated bee species in the crop can also be used if available

Low detail scenario

The low detail scenario was generated using only information related to the focal oilseed rape field. The field trials were conducted during flowering of the focal oilseed rape fields, corresponding to growth stages of the oilseed rape plants between BBCH 60 and 69. The flowering BBCH stages indicate the percentage of flowers open whereby peak flowering (BBCH 65) is reached when 50% of the flowers are open (Meier 2018; d'Andrimont et al. 2020). For the purpose of the floral resource assumptions in the SolBeePop input file, we assume that full flowering corresponds to optimal resource availability (Quality_crop = 1 in the model input) from the focal field. The floral resource availability at other growth stages was scaled to the percentage of flowers open of each BBCH stage. If a range of BBCH stages were reported in the Ruddle et al. (2018) study, the average between the highest and lowest of the range was used. For instance, BBCH 62 corresponds to 20% of flowers open in oilseed rape (d'Andrimont et al. 2020). If the plants in the field were reported to be in BBCH stages 62–65, it was assumed that, on average, 35% of flowers were open. Scaled to full flowering (BBCH 65 with 50% flowers open), this corresponds to the assumption that the proportional resource availability from the field corresponds to Quality_crop = 0.7. As BBCH stages were not reported for all days of the field study phase by Ruddle et al. (2018), the days without reported BBCH were interpolated linearly between the previous and following BBCH stage. Oilseed rape BBCH stages and the derived proportional resource availability from the crop are listed for each field study in Suppl. material 2: table S2–S7.

In the low detail scenario, detailed data related to the landscape and the pollen composition of bee provisions were not used and the simplifying assumption was applied that no resources were available other than the focal oilseed rape field. Accordingly, the resources from non-crop were set to 0 in the input file (Quality_nat = 0) corresponding to no foraging on resources other than crop (Prop_foraging_crop = 1).

Medium detail scenario

For the generation of the medium detail scenario, floral resources were considered that were available from the landscape in addition to the focal oilseed rape field. Landscape composition data were used that were specific to the study sites. Landscape composition data are available for many regions from public data bases although with varying resolution, detail in land-cover types and years for which the data can be retrieved. We used land-cover data from the European Union's Copernicus Land Monitoring Service Information, 'Corine Land Cover + Backbone' (CLC+Backbone) from 2018, with a 10 m resolution (European Environment Agency 2023). Data from this public inventory were available for all six study sites with the high spatial resolution. The dataset from 2018 was available at the time of our simulation study. Although the year does not correspond to the years when the field studies were conducted (2014 and 2015), the land covers were assumed to be constant over multiple years. In the Corine Land Cover data, raster cells with 10 m edge length are assigned to one of 11 classes (Table 3; see also Suppl. material 2: figs S3–S8 for the land-cover maps of the six sites).

Table 3. CLC+Backbone land cover classes (number and label from European Environment Agency 2023) and their assignment to floral resources used by *O. bicornis* in the SolBeePop application. –: no resources assumed (see comments in the table for details). NA: not applicable because land-cover type did not occur in analysed landscape areas.

Land-cover class	CLC+Backbone label	Plant taxa providing floral resources to *O. bicornis* assumed to correspond to the land-cover class	Comments
1	Sealed	–	No flowering plants assumed present
2	Woody needle leaved trees	–	Pollen from coniferous trees only reported in very few instances and low percentage in *O. bicornis* provisions
3	Woody broadleaved deciduous trees	Forest: *Quercus*, *Acer*, *Juglans*, *Aesculus*, *Salix* and other tree species; orchard: Rosaceae, including *Malus* (or Maleae), *Prunus*, *Rubus*	Includes deciduous and mixed forests as well as orchards
4	Woody broadleaved evergreen trees	NA	
5	Low-growing woody plants (bushes, shrubs)	–	Not included because only 0–2% of this land cover was present in the analysed landscape areas
6	Permanent herbaceous	Ranunculaceae and other herbaceous, non-crop plant taxa reported from *O. bicornis* provisions	Includes non-crop grassland such as meadows, grasslands managed for hay production and fallow fields
7	Periodically herbaceous	*Brassica napus* or Brassicaceae	Arable fields: according to the design of the field studies, no other flowering crops providing resources to *O. bicornis* were assumed present around the field sites
8	Lichens and mosses	NA	
9	Non- and sparsely vegetated	–	No resources assumed from flowering plants
10	Water	–	No resources assumed from flowering plants
11	Snow and ice	NA	

We assigned each land-cover type to plant taxa reported to be collected by *O. bicornis* (see Section Floral preferences of *O. bicornis*; Table 1). For the current study, we assumed that oilseed rape from the focal fields were the only non-permanent crop providing floral resources for *O. bicornis*. Different flowering times occur across the range of plant species potentially providing floral resources per land-cover type. In particular, many tree species flower early in the spring for a limited time period. Ranunculaceae and other herbaceous plants tend to start flowering later in the spring. Thus, we assumed different levels of floral resource availability from the non-crop resource-providing land-cover types. In addition, we assumed that the resource availability was dependent on time of year. In Table 3, we list the categorisation of resource availabilities applied per land-cover type and date range. The categorical assignments were based on reported flowering times of the plant taxa in Germany and the occurrence of their pollen in *O. bicornis* provisions. Details of the categorical assignments are provided in Suppl. material 2.

Table 4. Factors applied to the two non-crop land-cover types assumed to provide floral resources for *O. bicornis*. Factors were used irrespective of the simulated year.

Date range	Woody broadleaved deciduous trees	Permanent herbaceous
21 March – 20 April	0.67 (medium)	0.33 (low)
21 April – 20 May	1 (high)	0.33 (low)
21 May – 20 June	0.33 (low)	1 (high)

The land-cover composition was analysed within the presumed foraging radius of *O. bicornis* around the nest locations. Maximum foraging distances across multiple *Osmia* species were reported to range between 400 m and 1200 m (Greenleaf et al. 2007; Zurbuchen et al. 2010). Hofmann et al. (2020) reported average and maximum foraging distances in *O. bicornis* of 100 m and 250 m, respectively. Bednarska et al. (2022) found high percentages of oak (*Quercus*) pollen in sampled *O. bicornis* provisions and identified the nearest oak tree from each study location. The furthest distance between *O. bicornis* nest locations and an oak tree was 810 m, suggesting that the bees' maximum foraging ranges extend at least to that distance. As the reported foraging distances of *O. bicornis* (and *Osmia* in general) varied considerably between publications, we included three radii around the Ruddle et al. (2018) study locations in the analysis of the land cover: 400 m, 800 m and 1200 m.

We translated the land-covers within each foraging radius to model input time series using two approaches: based on distance to the nearest land-cover patch with resources ("dist") or based on the proportion of area with resource-providing land-covers ("prop"). For "dist", the minimum distance, d, (within the applicable foraging radius, r) was determined for each of the land-cover types providing non-crop floral resources, woody broadleaved deciduous trees and permanent herbaceous. As a generic proxy for the resource quality dependent on distance, we calculated $q = 1 - d/r$ for each land-cover type. In case the land-cover type did not occur within the foraging radius, q was set to 0. We then multiplied q with the factor from Table 3 corresponding to the date. The maximum of the two resulting values was used in the input time series Quality_nat. Thus, "dist" is a simplification of the landscape that only considers the land-cover that provides bee resources closest to the nest location. It corresponds to the simplifying assumption that the bees forage in one resource patch on a given day and that the resource availability is not limited by patch size. For the input files generated using "prop", the area of each of the two relevant land-covers within the foraging radius was divided by the total area. The proportion was then multiplied by the factor listed in Table 3 for each day. The sum of the two resulting numbers was used in the input time series Quality_nat. Accordingly, "prop" reflects the simplifying assumption that bees use multiple resource patches within their foraging radius on any given day and that resource availability is linked directly to patch size. Note that, for all study sites, at least one of the land-covers occurred within 400 m radius, i.e. Quality_nat > 0 for all study-specific inputs during the field phases for both "dist" and "prop". See also Suppl. material 2: tables S13, S14 for the summary of the land-cover distances and proportions per site.

High detail scenario

For the generation of input files for the high detail scenario, study-specific data on pollen composition of brood provisions were used whereby the provisions were sampled 3–4 times during the field phase of the studies (Ruddle et al. 2018). In the three studies conducted in 2014, samples were taken from unfinished brood cells on three dates during the field phase. Pollen was identified as *Brassica napus*, *Quercus* or other and the percentage in the samples of each were reported. In 2015, two sites were sampled four times (S15-01802, Niefern and S15-01803, Tübingen) and one was sampled three times (S15-01803,

Celle). Pollen was identified as *Brassica*, *Quercus*, *Acer*, *Ranunculus*, *Juglans*, *Aesculus*, Rosaceae, *Ligustrum* or other. Detailed pollen composition data from Ruddle et al. (2018) can be found in Suppl. material 1.

The percentage of *Brassica* pollen reported in the provisions was assumed to directly reflect the proportion of foraging on crop by the bees. The days between pollen samples were interpolated linearly to generate the daily values of 'Prop_foraging_crop' time series in the input file. As pollen provisions were not sampled on the first and last day of the field study phase, we assumed that, on the first day of the field phase, half of the proportion of *Brassica* pollen reported on the earliest sampling date applies to the proportion of foraging on crop. For the last day, we assumed that half of the proportion of *Brassica* pollen reported on the latest sampling date applied to the proportion of foraging on crop. The generic assumptions of half the proportion of Brassica pollen of the subsequent or previous sampling, respectively, reflects that oilseed rape was flowering at the start of the field phase in the field studies and the field phase was ended when oilseed rape flowering was coming to an end. These assumptions were necessary to allow interpolation of proportion of foraging on crop for all days during the study field phases.

Although the pollen composition data of the brood provisions provided study-specific data, it cannot be derived from the data to what extent each floral species was available in the landscape, its distance from the nest or the bees' effort involved in extracting the resource from the flowers. As this information was lacking, we used the same information and assumptions as in the medium detail scenario about the resource availability, based on proportions of relevant land-cover types within the foraging radius ("prop") or smallest distance from the nest ("dist"), respectively (see also Table 2).

Weather-dependent foraging

Weather is an important factor in the reproductive output of solitary bees: if the weather prevents nesting females from foraging, they cannot provision offspring. Weather conditions allowing foraging vary between species (Stubbs et al. 1994; Vicens and Bosch 2000; Drummond 2016). In the SolBeePop model, we assume that the life span of bees is independent of weather and, thus, lost time for brood cell production due to inclement weather cannot be compensated for by individual simulated bees. For *O. bicornis*, published data on weather-dependent foraging are limited. In a study with *O. bicornis*, no foraging activity was reported at temperatures below 10 °C, during rain and strong wind (Franke et al. 2021). The study was not focused on weather-dependent foraging and no further details were addressed. In a study focused on blueberry pollination, no bee activity from any species was observed on days with precipitation of 25.4 mm or more (Drummond 2016; Drummond et al. 2017). As default, we assumed that days with maximum measured air temperatures < 10 °C did not allow foraging by *O. bicornis*, as well as days with precipitation ≥ 25.4 mm (Prop_foraging_day = 0). No other weather conditions were considered and all days with maximum temperatures above the temperature threshold and below the precipitation threshold were assumed to allow foraging (Prop_foraging_day = 1). Given that these thresholds were based on unspecific data, we tested an alternative set of plausible thresholds for weather-dependent foraging. Seidelmann et al. (2010) used weather-dependent foraging thresholds for an analysis of *O. bicornis* study data. Although the authors

did not specify the sources for their assumptions, we used their assumptions as a plausible alternative scenario of weather-dependent foraging in the species. The assumed thresholds by Seidelmann et al. (2010) addressed air temperature (18 °C) and relative air humidity (60%). We applied 18 °C as minimum temperature threshold for foraging whereby we compared it to the maximum daily air temperature. Similarly, as a condition for foraging, the minimum daily relative humidity had to be 60% or less. As no threshold for precipitation was defined by Seidelmann et al. (2010), we used the threshold of 25.4 mm for this scenario as well.

Simulations with SolBeePop

Separate input files were generated for each scenario and study, defining the five daily time series (Table 2). Thereby, six input files per study were generated to represent the medium and high detail scenarios because two versions of representing the landcovers ("dist" and "prop") and three alternative foraging radii (400 m, 800 m and 1200 m) were applied as alternatives. For the exploration of weather-dependent foraging, we conducted additional simulations using one study (Tübingen 2015), combined with the low detail scenario and the high detail scenario "dist" with 1200 m foraging radius. The input files for these simulations were generated using different assumptions about weather-related foraging in *O. bicornis*. Model parameter settings corresponded to trait values for *O. bicornis* derived from literature and addressed in Schmolke et al. (2023). For a subset of parameters, average values were used that reflect the calibration of SolBeePop to semi-field study data with *O. bicornis*. The semi-field studies were conducted in 2015 at the same study locations as the 2015 field studies used in the current paper (Ruddle et al. 2018). The calibration to the semi-field studies was reported in Schmolke et al. (2023) and can also be found in Schmolke (2025). Study-specific dates were used in the simulations of each study, including the introduction of the *O. bicornis* cocoons at the nest boxes and the end of the field phase (when nest boxes were closed and further brood cell production was prevented). The parameters and settings used for the simulation and the input files are listed in Suppl. material 2: tables S11, S12, respectively. Each combination of study and scenario was simulated using 50 repetitions, i.e. simulations that differed only in the random number seeds and covering the stochasticity of the model.

For each simulation set (of 50 repetitions), we calculated the average, minimum and maximum outputs for number of post-emergent females and cumulative brood cells produced. For the comparison of the simulations to the study data, we calculated normalised root mean square errors (NRMSE). We used the NRMSE to identify the scenarios that corresponded best to the cumulative brood cell production observed in the field studies. For the generation of model input files, model output analysis and plotting, we used R (R Core Team 2022). Scripts and inputs and are provided in Schmolke (2025).

Results

In the simulations of the field studies, the different scenarios applied resulted in considerably different brood production rates. In the low detail scenario, floral resources were limited to the flowering oilseed rape. Flowering of the crop decreased towards the end of the field phases of the studies, with no flowering

of oilseed rape occurring in most studies prior to the end of the field phase. Accordingly, simulated bees were limited to provisioning brood during oilseed rape flowering, resulting in low offspring production towards the end of the simulated field phases. In contrast, the medium and high detail scenarios considered resources available beyond the focal oilseed rape field and simulations resulted in continued brood cell production until the end of the field phase. The simulated cumulative brood produced by the end of the field phases increased across scenarios, i.e. from the low to medium to high detail scenario (Fig. 1A).

For medium and high detail scenarios, we generated alternative versions to capture the uncertainty about the foraging distance of *O. bicornis* females around their nest, using 400 m, 800 m and 1200 m radii. In addition, we tested two alternative scenarios that were based on the proportional area ("prop") providing floral resources within the foraging or the distance ("dist") to the nearest patch, respectively. Using "prop" to estimate resource availability in the landscape resulted in much lower assumed relative resource availability in the landscapes compared to "dist". Correspondingly, simulations using medium or high detail scenarios, "prop" resulted in lower brood production rates that were more comparable to the low detail scenario (Fig. 1B). The assumed foraging radius was less impactful to the simulation outcomes (Fig. 1C). This applies to the simulations of the other sites as well (data not shown).

When comparing the simulation outputs to the field study data, the best relative match (lowest NRMSE) was obtained using the high detail scenario "dist" with a foraging radius of 1200 m. The study Tübingen 2014 was an exception whereby the simulations using this scenario vastly overestimated the observed total brood cell production (Fig. 2).

Whether or not foraging was possible on a specific day due to weather was also defined in model input. On a day without any foraging, nesting females did not produce offspring in the model. To test the importance of assumptions about the weather conditions allowing *O. bicornis* foraging, we conducted simulations for one study site that used different assumptions (thresholds) defining what weather conditions allow foraging in *O. bicornis*. Thereby, the second set of simulations assumed requirements for warmer and drier weather conditions (W2) compared to the first set (W1). Assumptions of W1 were used in all other simulations presented in the current paper. The second set of weather-related foraging assumptions resulted in fewer days available for foraging during the trial's field phase and, in turn, in lower brood cell production in the simulations (Fig. 3).

Discussion

From the perspective of a solitary bee foraging for pollen and nectar, the landscape surrounding its nest is a mosaic of patches with various levels of resources that change with the bloom of trees, meadows and crops. Floral resources are a direct driver of reproductive output (Kim 1999; Goodell 2003; Bosch and Vicens 2005, 2006; Peterson and Roitberg 2006a, 2006b) and, thus, population dynamics in solitary bees. In addition, the use of floral resources by a species over time and space are also important drivers of potential exposures to pesticides. In the current paper, we demonstrated how the aggregation of resources in a realistic landscape can be conducted to provide information for simulations with SolBeePop. We simulated field studies conducted with *O. bicornis*

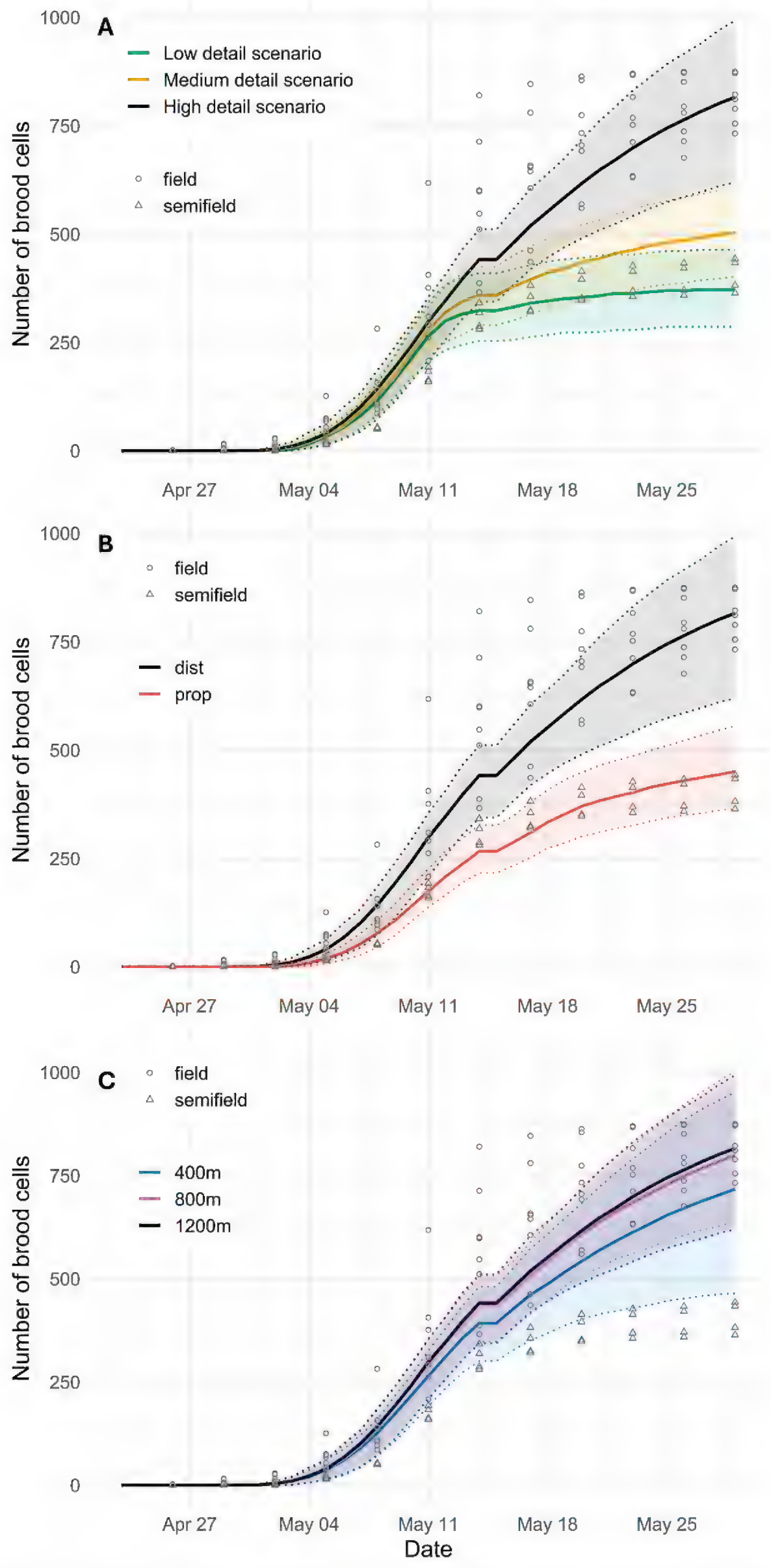

Figure 1. Comparison of simulated cumulative brood cells produced for the representation of the same landscape (Tübingen 2015). **A** Low, medium and high detail scenarios with "dist" and 1200 m foraging radius used with the medium and high detail scenarios; **B** distance ("dist") or proportional area ("prop") to estimate floral resource availability in the landscape with the high detail scenario using 1200 m foraging radius; **C** foraging radii of 400 m, 800 m or 1200 m with the high detail scenario using "dist". Solid lines indicate averages of 50 simulations, shaded areas the ranges between minimum and maximum. Data from the corresponding field and semi-field studies are shown as circles and triangles, respectively.

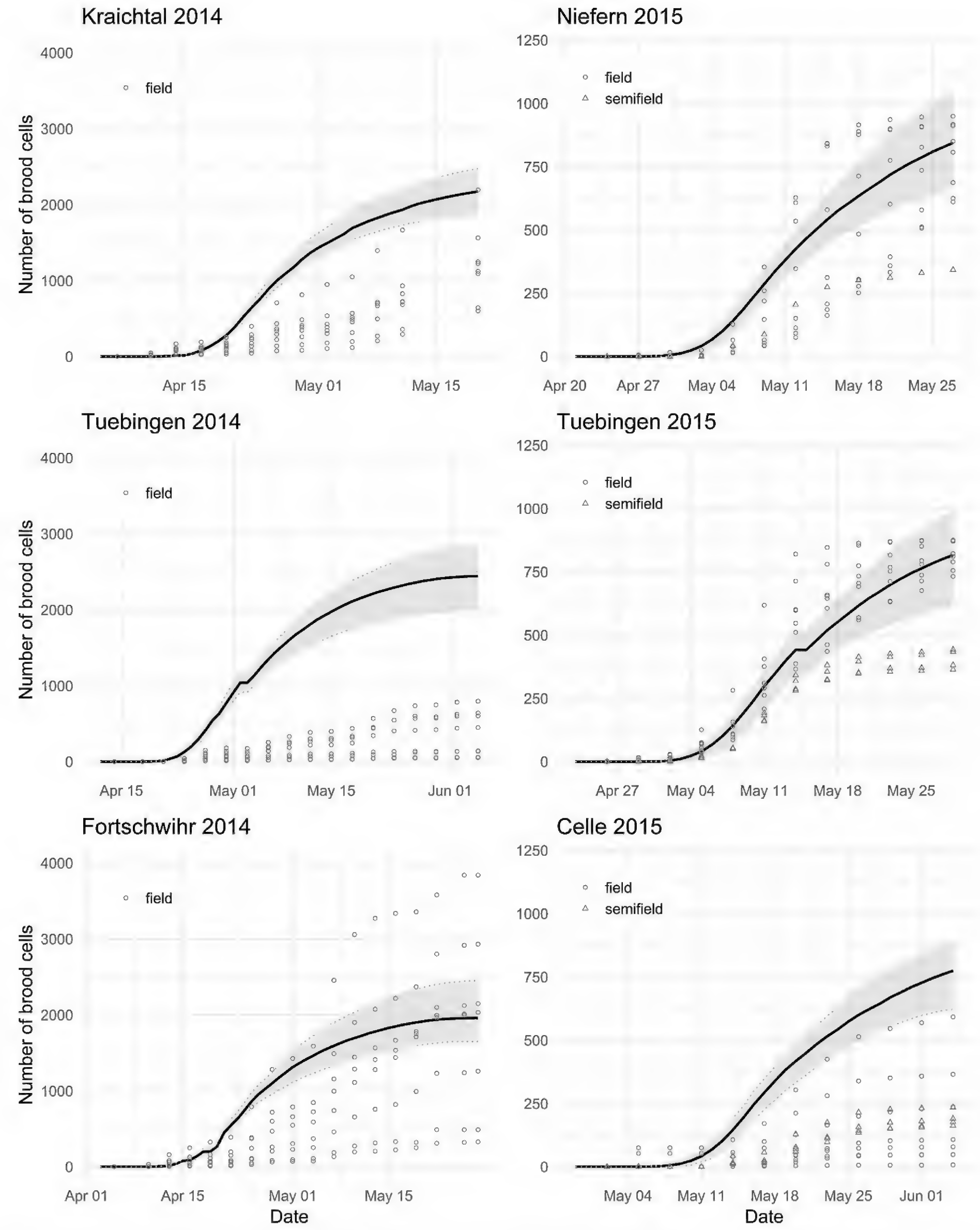

Figure 2. Cumulative brood cell production for the six studies. Average simulated brood cell numbers are shown as black lines, minimum and maximum as grey lines. Dots indicate the study data whereby triangles indicate data from semi-field trials conducted in 2015 (right column) which are not directly comparable to the simulations. Solid black lines indicate averages of 50 simulations (high detail scenario, dist, 1200 m foraging radius), shaded areas the ranges between minimum and maximum. Data from the corresponding field and semi-field studies are shown as circles and triangles, respectively. Semi-field studies were only conducted in 2015. Note that the y-axis limits were chosen differently for the two study years because different numbers of cocoons were introduced at the sites.

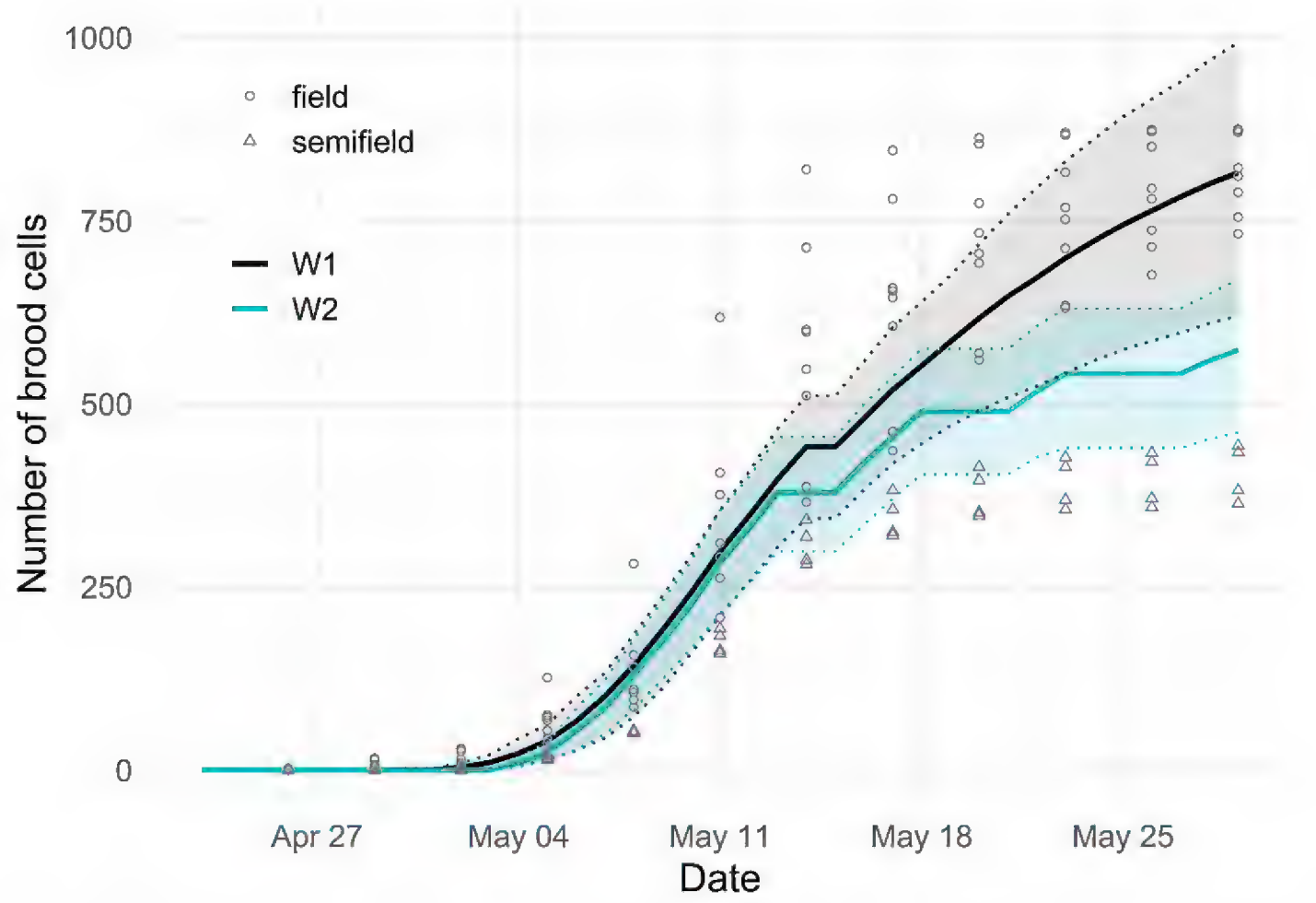

Figure 3. Comparison of simulated cumulative brood cells produced using two different time series for weather-related foraging (Tübingen 2015). W1: default assumptions about weather-related foraging. W2: assumptions from Seidelmann et al. (2010). Floral resources were represented using the high detail scenario, dist, 1200 m foraging radius. Solid lines indicate averages of 50 simulations, shaded areas the ranges between minimum and maximum. Data from the corresponding field and semi-field studies are shown as circles and triangles, respectively.

(Ruddle et al. 2018) and compared model outputs to (untreated) control data. Thus, we could address whether the model captures nesting and brood production observed in the control fields of the studies and how increased detail providing information for the landscape input can improve model performance.

Ruddle et al. (2018) conducted semi-field studies in the second study year (2015) in addition to the field trials. In semi-field studies, bees are limited to foraging on a section of an oilseed rape field under a mesh tent. Brood cell production in those studies was lower than in the corresponding field trials at two sites (Niefern 2015; Tübingen 2015), particularly during the second half of the (semi-) field phase. At the third site (Celle 2015), brood production was low across most nest boxes, with the semi-field trials falling within the field trial data. The semi-field study design corresponded to the simplifying assumption applied to the model inputs in the low detail scenario, resulting in smaller brood cell production than observed in the field studies and model simulations in scenarios with more detail included.

The simulated cumulative brood cell production increased with increasingly detailed information used for the scenario development. The medium detail scenario incorporated the aggregated representation of the landscape surrounding each study site, capturing floral resources available beyond the focal crop fields. In the high detail scenario, we additionally used study-specific pollen composition data to derive the proportion of foraging on crop vs. non-crop. While oilseed rape pollen was present in the samples (0–58.4%), its percentage differed by study site and sampling date. Oilseed rape peak flowering (BBCH 65) was limited to about a week, indicating that the resources from oilseed

rape were not optimal throughout the field study phases and floral resources beyond the focal field were important drivers of brood production. In addition, *O. bicornis* appears to seek out oak pollen specifically, even if nest boxes are placed adjacent to flowering oilseed rape fields (Bednarska et al. 2022).

With the use of different levels of detail to generate model input scenarios, we demonstrated how information on landscapes can be aggregated to provide information for modelling. Thereby, the detail of information that can be represented does not only depend on landscape composition data, but also on information about the bees' floral preferences, i.e. their potential use of the landscape. For *O. bicornis*, preferences have been reported in literature. Our compilation of *O. bicornis* preferences (derived from pollen compositions of brood provisions) identify preferences independent of region, but also indicate the large range of plants that the species uses. Thus, the pollen collected likely strongly depends on relative availabilities of different floral resources over time. In addition, the pollen nutrition content may play a role, but was not addressed in the reviewed studies. For the studies simulated in the current paper, pollen compositions of the brood provisions were also quantified. While we show that this level of information can improve the accuracy of the simulations, considerable variability in the field study data remains which is not explained by the model. The observed variability may originate from multiple factors, including specific weather patterns and fine-scale resource availabilities. In addition, the variability within studies also points to unknown factors influencing outcomes of field studies. This variability in the field study data means that it is difficult to determine a best fitting scenario with the model. For instance, brood cell numbers in the trial Tübingen 2014 were particularly low, resulting in a stark overestimation by the model using the scenario that performed best across trials. Reasons for the low brood production rates in that trial (and also relatively low brood production rates in Kraichtal 2014 and Celle 2015) are not reported in the study (Ruddle et al. 2018). Multiple factors can contribute to such variability, including but not limited to the condition of the released cocoons and the dispersal of the bees. While the model can represent variability in weather-dependent foraging conditions and resource availability in the landscape, their impact on survival or dispersal decisions of emerged bees are unclear and not included in the model.

We demonstrated how different levels of information about the landscape and species' preferences can provide information for modelling and decision-making. In case of lacking information on species' preferences as well as resource distributions in time and space, simplified scenarios can be generated and tested with the model. These correspond to the low detail scenario tested which resulted in low brood production, representing a more conservative option, even under control conditions. If potential exposures to pesticides are being addressed, additional conservative assumptions can help to provide information for relevant scenarios, for example, assuming high levels of foraging on the exposed crop while it is in flower. Once more detailed data are available, the realism of the landscape representation can be increased accordingly which is crucial when assessing whether landscapes could provide sufficient resources to sustain populations of solitary bee species. Particularly for polylectic species, such as *O. bicornis*, that are reported to use multiple floral sources in parallel, treated and untreated resources present in a landscape should be considered to estimate realistic exposures to pesticides (EFSA et al. 2023). The

aggregated landscape representation used by SolBeePop provides the option to capture temporal and spatial variability in resources even if a bee's use of the landscape is not known in detail. We would like to note that for oligolectic species, a simple landscape representation is even more appropriate because the relevant floral resources should be expected to occur only in a single land-cover type. Thus, scenarios corresponding to the low detail scenario in the current study are likely sufficient to capture resource availability in the landscape.

When generating scenarios using landscape composition data, it matters how the landscape composition is considered. In the current study, we calculated the proportion of resource-providing area relative to the entire area within the assumed foraging range. The proportion resulted in low estimates of resource availability and did not considerably increase simulated brood cell production rates compared to the low detail scenario. Rather, using the shortest distance from the nest location to the nearest resource resulted in higher assumed resource availabilities from non-crop resources and corresponding higher brood cell production. The scenarios using the distance to the nearest resource (dist) did not consider the area of that resource. In reality, the size of a resource patch, the density and quality of pollen available in the patch and competition from other bee species may all play a role. Thus, distance and area of resources patches may both play a role. Here, we contrast the two approaches of aggregating the landscape. Assuming a small resource patch can provide sufficient resources for solitary bees is plausible considering their low numbers, for example, compared to honey-bee foragers. In addition, solitary bees do not communicate about resources in the landscape and a single bee conducts a limited number of foraging flights per day (e.g. Bosch and Vicens (2005); Palladini and Maron (2014)). Thus, the proportion of area in the surrounding landscape providing resources is unlikely to be indicative of resource availability from the perspective of the bee. Rather, few attractive resources are likely sought out on a daily basis. The distance to these resources is an important factor because longer flight distances require more energy and time and have been shown to reduce reproductive output in solitary bees (Kim 1999; Goodell 2003; Bosch and Vicens 2005, 2006; Peterson and Roitberg 2006a, 2006b). This is also consistent with a study by Lonsdorf et al. (2024) who found that a statistical model could better explain data on residue levels observed in bumble bee-collected pollen in an agricultural landscape in California if season, distance and floral-weighted foraging behaviour were considered.

Multiple model approaches have been published addressing pollination services in agricultural landscapes (Rouabah et al. 2024). Many models focus on estimating the interaction between landscape fragmentation or estimates of other landscape indicators and pollination services, crop yield, bee abundance or diversity. However, pesticide exposures and effects are typically not included in most models, with the exception of those representing honey-bee colonies (Baveco et al. 2016; Garber et al. 2022; Preuss et al. 2022). For the understanding of potential exposures and effects of pesticides to populations of managed and unmanaged solitary bees, the representation of a species' ecology, including the life cycle and phenology, are important because they interact with risk of exposure as well as population-level effects. The risk of exposure to pesticides is mainly driven by the species-specific phenology, spatial behaviour and interaction with the landscape. In the current study, we addressed this gap in current available knowledge and methodology by

evaluating several options for landscape representation in a solitary bee population model, using data specific to a species.

In addition to landscape compositions, weather conditions have a major influence on foraging activity and, thus, reproduction of bees. Although *O. bicornis* is one of few solitary bee species that has been studied fairly extensively, published studies on its weather-related foraging preferences are limited. In the simulations with SolBeePop, we used thresholds defining weather-related foraging that were derived from studies addressing multiple bee species (not including *O. bicornis*) or in which weather conditions were not the focus of the study (Drummond 2016; Drummond et al. 2017; Franke et al. 2021). To address how assumptions about weather-related foraging affect simulation outputs, we applied alternative generic assumptions. The threshold temperature for foraging was assumed to be 10 °C or 18 °C, respectively and the threshold relative air humidity for foraging was either not considered or assumed 60%. The differences in assumed thresholds resulted in very different number of days assigned as available for foraging and, correspondingly, different simulation outputs. Thus, more detailed information on weather-dependent foraging in the species could improve the realism of the simulations. It would be relevant to define thresholds or correlations between foraging activity in a species and air temperature, relative air humidity, precipitation and wind speed. In addition, solar irradiation has also been stated as an important weather-related factor for bee foraging (Seidelmann et al. 2010). In the current application, we assigned days to be either fully available for foraging or not, based on thresholds, which corresponds to a simplifying assumption, appropriate when more detailed data are lacking. However, if species-specific data are available, relationships between weather conditions and foraging activity could be used on a higher temporal resolution (e.g. from hourly weather data). Durations of each day available for foraging could be derived, i.e. days could be partially available for foraging in the simulations.

Conclusions

Floral resources in agricultural landscapes and species-specific spatial behaviour are important drivers of bee population dynamics. However, phenologies and floral preferences of different bee species, as well as variability in resource availability in time and space, can make it challenging to represent landscapes from the perspective of bees. Ecological models provide a pathway to incorporate available data, as well as bridging knowledge gaps. In the current study, we demonstrate how different assumptions, based on different levels of detail of information on the landscape composition, as well as a bee's floral preferences, can be applied to generate scenarios for SolBeePop. The consideration of floral resources beyond the focal mass-flowering crop improved the performance of the model when compared to *O. bicornis* field study data. At the same time, scenarios using low and medium detail provided useful, more conservative model outputs. Such scenarios could be extended to generate conservative pesticide exposure scenarios and simulations could be evaluated for the assessment of risks to species with limited information. Exploring different scenarios can also provide information about what data are important to improve the realism in model simulations. In studies conducted with solitary bee species, the bees' foraging preferences are informative, as well as record-

ing weather conditions that allow foraging of the bees. At the same time, the model provides the possibility to represent bees for which these aspects are not well described. We demonstrated the application of the model in a landscape context for *O. bicornis*. This species is one of the very few polylectic solitary bee species with detailed data on its pollen preferences. Still, a lot of variability in its pollen preferences are apparent from our review and translating the preferences to land-use maps corresponds to a rough estimate. However, the simulations indicate that considering multiple floral resources increases the realism of the model outputs. Other bee species can be simulated considering the landscape with low or medium detail, even in the absence of detailed knowledge of their floral preferences. Thus, the current model represents an important tool for identifying data gaps and research needs, as well for supporting risk assessments of solitary bee species in complex landscapes.

Acknowledgements

Thanks to Natalie Ruddle for providing data and addressing questions about the field studies, Anna Persson for providing the data on O. bicornis provision compositions and Cynthia Camacho Munoz and Peter Vermeiren for the analysis of the landscape data. We also thank Charlotte Elston and three other reviewers who provided constructive reviews on an earlier version of this manuscript.

Additional information

Conflict of interest

Nika Galic works for Syngenta. Silvia Hinarejos works for Sumitomo. The work was funded by Sumitomo and Syngenta which produce and sell agrochemicals. All authors have an interest in getting SolBeePop accepted for regulatory purposes.

Ethical statement

No ethical statement was reported.

Funding

The work was funded by Sumitomo Chemical and Syngenta Crop Protection.

Author contributions

Silvia Hinarejos, Nika Galic and Amelie Schmolke developed the scenarios and details of the simulations. Amelie Schmolke conducted the simulations and analyses, provided the documentation and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Author ORCIDs

Amelie Schmolke https://orcid.org/0000-0002-8114-7287
Nika Galic https://orcid.org/0000-0002-4344-3464
Silvia Hinarejos https://orcid.org/0000-0003-0969-6799

Data availability

Model code, related files and documentation available from https://doi.org/10.5281/zenodo.15323914.

References

Accolla C, Vaugeois M, Grimm V, Moore AP, Rueda-Cediel P, Schmolke A, Forbes VE (2021) A review of key features and their implementation in unstructured, structured, and agent-based population models for ecological risk assessment. Integrated Environmental Assessment and Management 17: 521–540. https://doi.org/10.1002/ieam.4362

Ammann L, Bosem-Baillod A, Herzog F, Frey D, Entling MH, Albrecht M (2024) Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes. Agriculture, Ecosystems & Environment 359: 108754. https://doi.org/10.1016/j.agee.2023.108754

d'Andrimont R, Taymans M, Lemoine G, Ceglar A, Yordanov M, van der Velde M (2020) Detecting flowering phenology in oil seed rape parcels with Sentinel-1 and -2 time series. Remote Sensing of Environment 239: 111660. https://doi.org/10.1016/j.rse.2020.111660

Baveco JM, Focks A, Belgers D, Steen JJM van der, Boesten JJTI, Roessink I (2016) An energetics-based honeybee nectar-foraging model used to assess the potential for landscape-level pesticide exposure dilution. PeerJ 4: e2293. https://doi.org/10.7717/peerj.2293

Becher MA, Grimm V, Thorbek P, Horn J, Kennedy PJ, Osborne JL (2014) BEEHAVE: a systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure. Journal of Applied Ecology 51: 470–482. https://doi.org/10.1111/1365-2664.12222

Becher MA, Twiston-Davies G, Penny TD, Goulson D, Rotheray EL, Osborne JL (2018) Bumble-BEEHAVE: A systems model for exploring multifactorial causes of bumblebee decline at individual, colony, population and community level. Journal of Applied Ecology 55: 2790–2801. https://doi.org/10.1111/1365-2664.13165

Bednarska AJ, Mikołajczyk Ł, Ziółkowska E, Kocjan K, Wnęk A, Mokkapati JS, Teper D, Kaczyński P, Łozowicka B, Śliwińska R, Laskowski R (2022) Effects of agricultural landscape structure, insecticide residues, and pollen diversity on the life-history traits of the red mason bee *Osmia bicornis*. Science of The Total Environment 809: 151142. https://doi.org/10.1016/j.scitotenv.2021.151142

Bertrand C, Eckerter PW, Ammann L, Entling MH, Gobet E, Herzog F, Mestre L, Tinner W, Albrecht M (2019) Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. Journal of Applied Ecology 56: 2431–2442. https://doi.org/10.1111/1365-2664.13483

Bishop GA, Fijen TPM, Raemakers I, van Kats RJM, Kleijn D (2024) Bees go up, flowers go down: Increased resource limitation from late spring to summer in agricultural landscapes. Journal of Applied Ecology 61: 431–441. https://doi.org/10.1111/1365-2664.14576

Bosch J, Vicens N (2005) Sex allocation in the solitary bee *Osmia cornuta*: do females behave in agreement with Fisher's theory? Behavioral Ecology and Sociobiology 59: 124. https://doi.org/10.1007/s00265-005-0017-8

Bosch J, Vicens N (2006) Relationship between body size, provisioning rate, longevity and reproductive success in females of the solitary bee *Osmia cornuta*. Behavioral Ecology and Sociobiology 60: 26–33. https://doi.org/10.1007/s00265-005-0134-4

Bosch J, Maeta Y, Rust R (2001) A phylogenetic analysis of nesting behavior in the genus *Osmia* (Hymenoptera: Megachilidae). Annals of the Entomological Society of America 94: 617–627. https://doi.org/10.1603/0013-8746(2001)094[0617:APAONB]2.0.CO;2

Bosch J, Sgolastra F, Kemp WP (2008) Life cycle ecophysiology of *Osmia* mason bees used as crop pollinators. In: Bee Pollination in Agricultural Ecosystems. Oxford University Press, New York, 83–104. https://doi.org/10.1093/acprof:oso/9780195316957.003.0006

Bottero I, Dominik C, Schweiger O, Albrecht M, Attridge E, Brown MJF, Cini E, Costa C, De la Rúa P, de Miranda JR, Di Prisco G, Dzul Uuh D, Hodge S, Ivarsson K, Knauer AC, Klein A-M, Mänd M, Martínez-López V, Medrzycki P, Pereira-Peixoto H, Potts S, Raimets R, Rundlöf M, Schwarz JM, Senapathi D, Tamburini G, Talaván ET, Stout JC (2023) Impact of landscape configuration and composition on pollinator communities across different European biogeographic regions. Frontiers in Ecology and Evolution 11: 1128228. https://www.frontiersin.org/articles/10.3389/fevo.2023.1128228 [May 18, 2023]

Cripps C, Rust RW (1989) Pollen preferences of seven *Osmia* species (Hymenoptera: Megachilidae). Environmental Entomology 18: 133–138. https://doi.org/10.1093/ee/18.1.133

Danforth BN, Minckley RL, Neff JL (2019) The Solitary Bees. Biology, Evolution, Conservation. Princeton University Press, Princeton, NJ, USA. https://doi.org/10.1515/9780691189321

De Palma A, Kuhlmann M, Roberts SPM, Potts SG, Börger L, Hudson LN, Lysenko I, Newbold T, Purvis A (2015) Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. Journal of Applied Ecology 52: 1567–1577. https://doi.org/10.1111/1365-2664.12524

Drummond FA (2016) Behavior of bees associated with the wild blueberry agro-ecosystem in the USA. International Journal of Entomology and Nematology 2: 27–42.

Drummond FA, Dibble AC, Stubbs C, Bushmann SL, Ascher JS, Ryan J (2017) A natural history of change in native bees associated with lowbush blueberry in Maine. Northeastern Naturalist 24: 49–68. https://doi.org/10.1656/045.024.m1502

EFSA, Adriaanse P, Arce A, Focks A, Ingels B, Jölli D, Lambin S, Rundlöf M, Süßenbach D, Del Aguila M, Ercolano V, Ferilli F, Ippolito A, Szentes C, Neri FM, Padovani L, Rortais A, Wassenberg J, Auteri D (2023) Revised guidance on the risk assessment of plant protection products on bees (*Apis mellifera*, *Bombus* spp. and solitary bees). EFSA Journal 21: e07989. https://doi.org/10.2903/j.efsa.2023.7989

European Environment Agency (2023) CLC+Backbone 2018 (raster 10 m), Europe, 3-yearly, Feb. 2023. https://doi.org/10.2909/cd534ebf-f553-42f0-9ac1-62c1dc36d32c

Franke L, Elston C, Jütte T, Klein O, Knäbe S, Lückmann J, Roessink I, Persigehl M, Cornement M, Exeler N, Giffard H, Hodapp B, Kimmel S, Kullmann B, Schneider C, Schnurr A (2021) Results of 2-year ring testing of a semifield study design to investigate potential impacts of plant protection products on the solitary bees *Osmia bicornis* and *Osmia cornuta* and a proposal for a suitable test design. Environmental Toxicology and Chemistry 40: 236–250. https://doi.org/10.1002/etc.4874

Garber K, DeGrandi-Hoffman G, Curry R, Minucci JM, Dawson DE, Douglass C, Milone JP, Purucker ST (2022) Simulating the effects of pesticides on honey bee (*Apis mellifera* L.) colonies with BeePop+. Ecologies 3: 275–291. https://doi.org/10.3390/ecologies3030022

Goodell K (2003) Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. Oecologia 134: 518–527. https://doi.org/10.1007/s00442-002-1159-2

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153: 589–596. https://doi.org/10.1007/s00442-007-0752-9

Gresty CEA, Clare E, Devey DS, Cowan RS, Csiba L, Malakasi P, Lewis OT, Willis KJ (2018) Flower preferences and pollen transport networks for cavity-nesting solitary bees: Implications for the design of agri-environment schemes. Ecology and Evolution 8: 7574–7587. https://doi.org/10.1002/ece3.4234

Grimm V, Railsback SF (2005) Individual-based Modeling and Ecology. Princeton University Press, 428 pp. https://doi.org/10.1515/9781400850624

Haider M, Dorn S, Sedivy C, Müller A (2014) Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees (Megachilidae: Osmiini). Biological Journal of the Linnean Society 111: 78–91. https://doi.org/10.1111/bij.12186

Hopfenmüller S, Steffan-Dewenter I, Holzschuh A (2014) Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. PLOS ONE 9: e104439. https://doi.org/10.1371/journal.pone.0104439

Jauker F, Peter F, Wolters V, Diekötter T (2012) Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outbalance post-flowering disadvantages. Basic and Applied Ecology 13: 268–276. https://doi.org/10.1016/j.baae.2012.03.010

Killewald M, Rowe L, Graham K, Wood T, Isaacs R (2019) Use of nest and pollen resources by leafcutter bees, genus *Megachile* (Hymenoptera: Megachilidae) in Central Michigan. The Great Lakes Entomologist 52. https://doi.org/10.22543/0090-0222.2338

Kim J (1999) Influence of resource level on maternal investment in a leaf-cutter bee (Hymenoptera: Megachilidae). Behavioral Ecology 10: 552–556. https://doi.org/10.1093/beheco/10.5.552

Knapp JL, Nicholson CC, Jonsson O, de Miranda JR, Rundlöf M (2023) Ecological traits interact with landscape context to determine bees' pesticide risk. Nature Ecology & Evolution 7: 547–556. https://doi.org/10.1038/s41559-023-01990-5

Lau PW, Esquivel IL, Parys KA, Hung K-LJ, Chakrabarti P (2023) The nutritional landscape in agroecosystems: a review on how resources and management practices can shape pollinator health in agricultural environments. Annals of the Entomological Society of America 116: 261–275. https://doi.org/10.1093/aesa/saad023

Lonsdorf EV, Rundlöf M, Nicholson CC, Williams NM (2024) A spatially explicit model of landscape pesticide exposure to bees: Development, exploration, and evaluation. Science of The Total Environment 908: 168146. https://doi.org/10.1016/j.scitotenv.2023.168146

Mandelik Y, Winfree R, Neeson T, Kremen C (2012) Complementary habitat use by wild bees in agro-natural landscapes. Ecological Applications 22: 1535–1546. https://doi.org/10.1890/11-1299.1

Meier U [Ed.] (2018) Growth stages of mono-and dicotyledonous plants. BBCH Monograph. https://www.openagrar.de/servlets/MCRFileNodeServlet/openagrar_derivate_00016780/BBCH%20ENGLISCH_%20.pdf [July 11, 2023]

Misiewicz A, Mikołajczyk Ł, Bednarska AJ (2023) Floral resources,energetic value and pesticide residues in provisions collected by *Osmia bicornis* along a gradient of oilseed rape coverage. Scientific Reports 13: 13372. https://doi.org/10.1038/s41598-023-39950-5

Nagamitsu T, Suzuki MF, Mine S, Taki H, Shuri K, Kikuchi S, Masaki T (2018) Effects of forest loss and fragmentation on pollen diets and provision mass of the mason bee, *Osmia cornifrons*, in central Japan. Ecological Entomology 43: 245–254. https://doi.org/10.1111/een.12494

Nicholson CC, Lonsdorf EV, Andersson GKS, Knapp JL, Svensson GP, Gönczi M, Jonsson O, de Miranda JR, Williams NM, Rundlöf M (2024) Landscapes of risk: A comparative analysis of landscape metrics for the ecotoxicological assessment of pesticide

risk to bees. Journal of Applied Ecology 61: 975–986. https://doi.org/10.1111/1365-2664.14622

O'Neill KM, O'Neill RP, Blodgett S, Fultz J (2004) Composition of pollen loads of *Megachile rotundata* in relation to flower diversity (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 77: 619–625. https://doi.org/10.2317/E-24.1

O'Neill RP, O'Neill KM (2011) Pollen load composition and size in the leafcutting bee *Megachile rotundata* (Hymenoptera: Megachilidae). Apidologie 42: 223–233. https://doi.org/10.1051/apido/2010057

Palladini JD, Maron JL (2014) Reproduction and survival of a solitary bee along native and exotic floral resource gradients. Oecologia 176: 789–798. https://doi.org/10.1007/s00442-014-3028-1

Persson AS, Mazier F, Smith HG (2018) When beggars are choosers—How nesting of a solitary bee is affected by temporal dynamics of pollen plants in the landscape. Ecology and Evolution 8: 5777–5791. https://doi.org/10.1002/ece3.4116

Peters B, Gao Z, Zumkier U (2016) Large-scale monitoring of effects of clothianidin-dressed oilseed rape seeds on pollinating insects in Northern Germany: effects on red mason bees (*Osmia bicornis*). Ecotoxicology 25: 1679–1690. https://doi.org/10.1007/s10646-016-1729-4

Peterson JH, Roitberg BD (2006a) Impact of resource levels on sex ratio and resource allocation in the solitary bee, *Megachile rotundata*. Environmental Entomology 35: 1404–1410. https://doi.org/10.1093/ee/35.5.1404

Peterson JH, Roitberg BD (2006b) Impacts of flight distance on sex ratio and resource allocation to offspring in the leafcutter bee, *Megachile rotundata*. Behavioral Ecology and Sociobiology 59: 589–596. https://doi.org/10.1007/s00265-005-0085-9

Preuss TG, Agatz A, Goussen B, Roeben V, Rumkee J, Zakharova L, Thorbek P (2022) The BEEHAVEecotox Model—Integrating a mechanistic effect module into the honeybee colony model. Environmental Toxicology and Chemistry 41: 2870–2882. https://doi.org/10.1002/etc.5467

R Core Team (2022) R: A Language and Environment for Statistical Computing. https://www.R-project.org/

Raw A (1974) Pollen preferences of three *Osmia* species (Hymenoptera). Oikos 25: 54–60. https://doi.org/10.2307/3543545

Riggi LGA, Raderschall CA, Fijen TPM, Scheper J, Smith HG, Kleijn D, Holzschuh A, Aguilera G, Badenhausser I, Bänsch S, Beyer N, Blitzer EJ, Bommarco R, Danforth B, González-Varo JP, Grab H, Le Provost G, Poveda K, Potts SG, Rundlöf M, Steffan-Dewenter I, Tscharntke T, Vilà M, Westphal C, Berggren Å, Lundin O (2024) Early-season mass-flowering crop cover dilutes wild bee abundance and species richness in temperate regions: A quantitative synthesis. Journal of Applied Ecology 61: 452–464. https://doi.org/10.1111/1365-2664.14566

Rouabah A, Rabolin-Meinrad C, Gay C, Therond O (2024) Models of bee responses to land use and land cover changes in agricultural landscapes – a review and research agenda. Biological Reviews 99: 2003–2021. https://doi.org/10.1111/brv.13109

Ruddle N, Elston C, Klein O, Hamberger A, Thompson H (2018) Effects of exposure to winter oilseed rape grown from thiamethoxam-treated seed on the red mason bee *Osmia bicornis*. Environmental Toxicology and Chemistry 37: 1071–1083. https://doi.org/10.1002/etc.4034

Ryder J (2019) The importance of nutrition for bumblebees and solitary bees; implications for pesticides and stewardship. PhD Thesis. [Harper Adams University Available from:] https://hau.repository.guildhe.ac.uk/id/eprint/17462/1/Jordan%20Ryder.pdf

Scheper J, Bommarco R, Holzschuh A, Potts SG, Riedinger V, Roberts SPM, Rundlöf M, Smith HG, Steffan-Dewenter I, Wickens JB, Wickens VJ, Kleijn D (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. Journal of Applied Ecology 52: 1165–1175. https://doi.org/10.1111/1365-2664.12479

Schmolke A (2025) SolBeePop/SolBeePop: v2.1.0. https://doi.org/10.5281/zenodo.15323914

Schmolke A, Abi-Akar F, Hinarejos S (2019) Honey bee colony-level exposure and effects in realistic landscapes: An application of BEEHAVE simulating clothianidin residues in corn pollen. Environmental Toxicology and Chemistry 38: 423–435. https://doi.org/10.1002/etc.4314

Schmolke A, Galic N, Hinarejos S (2023) SolBeePop: A model of solitary bee populations in agricultural landscapes. Journal of Applied Ecology 60: 2573–2585. https://doi.org/10.1111/1365-2664.14541

Schmolke A, Galic N, Roeben V, Preuss TG, Miles M, Hinarejos S (2024) SolBeePopecotox: A population model for pesticide risk assessments of solitary bees. Environmental Toxicology and Chemistry 43: 2645–2661. https://doi.org/10.1002/etc.5990

Seidelmann K, Ulbrich K, Mielenz N (2010) Conditional sex allocation in the Red Mason bee, *Osmia rufa*. Behavioral Ecology and Sociobiology 64: 337–347. https://doi.org/10.1007/s00265-009-0850-2

Šlachta M, Erban T, Votavová A, Bešta T, Skalský M, Václavíková M, Halešová T, Edwards-Jonášová M, Včeláková R, Cudlín P (2020) Domestic gardens mitigate risk of exposure of pollinators to pesticides—An urban-rural case study using a red mason bee species for biomonitoring. Sustainability 12: 9427. https://doi.org/10.3390/su12229427

Söderman AME, Irminger Street T, Hall K, Olsson O, Prentice HC, Smith HG (2018) The value of small arable habitats in the agricultural landscape: Importance for vascular plants and the provisioning of floral resources for bees. Ecological Indicators 84: 553–563. https://doi.org/10.1016/j.ecolind.2017.09.024

Splitt A, Skórka P, Strachecka A, Borański M, Teper D (2021) Keep trees for bees: Pollen collection by *Osmia bicornis* along the urbanization gradient. Urban Forestry & Urban Greening 64: 127250. https://doi.org/10.1016/j.ufug.2021.127250

St. Clair AL, Zhang G, Dolezal AG, O'Neal ME, Toth AL (2020) Diversified farming in a monoculture landscape: Effects on honey bee health and wild bee communities. Environmental Entomology 49: 753–764. https://doi.org/10.1093/ee/nvaa031

Stubbs CS, Drummond FA, Osgood EA (1994) *Osmia ribifloris* biedermannii and *Megachile rotundata* (Hymenoptera: Megachilidae) introduced into the lowbush blueberry agroecosystem in Maine. Journal of the Kansas Entomological Society 67: 173–185.

Teper D (2008) Food plants of *Megachile rotundata* L. determined based on palinological analysis of faeces. Journal of Apicultural Science 52: 73–80.

Teper D, Bilinski M (2009) Red mason bee (*Osmia rufa* L.) as a pollinator of rape plantations. Journal of Apicultural Science 53: 115–120.

Vaudo AD, Biddinger DJ, Sickel W, Keller A, López-Uribe MM (2020) Introduced bees (*Osmia cornifrons*) collect pollen from both coevolved and novel host-plant species within their family-level phylogenetic preferences. Royal Society Open Science 7: 200225. https://doi.org/10.1098/rsos.200225

Vicens N, Bosch J (2000) Weather-dependent pollinator activity in an apple orchard, with special reference to *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae and Apidae). Environmental Entomology 29: 413–420. https://doi.org/10.1603/0046-225X-29.3.413

Yourstone J, Karlsson M, Klatt BK, Olsson O, Smith HG (2021) Effects of crop and non-crop resources and competition: High importance of trees and oilseed rape for solitary bee reproduction. Biological Conservation 261: 109249. https://doi.org/10.1016/j.biocon.2021.109249

Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143: 669–676. https://doi.org/10.1016/j.biocon.2009.12.003

Supplementary material 1

Excel tables with detailed compilation of *O. bicornis* floral preferences

Authors: Amelie Schmolke

Data type: xlsx

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/https://doi.org/10.3897/fmj.6.149273.suppl1

Supplementary material 2

Tables and descriptions of field study data and simulations

Authors: Amelie Schmolke

Data type: pdf

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/https://doi.org/10.3897/fmj.6.149273.suppl2